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Vector navigation in desert ants, *Cataglyphis fortis*: celestial compass cues are essential for the proper use of distance information

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Abstract Foraging desert ants navigate primarily by path integration. They continually update homing direction and distance by employing a celestial compass and an odometer. Here we address the question of whether information about travel distance is correctly used in the absence of directional information. By using linear channels that were partly covered to exclude celestial compass cues, we were able to test the distance component of the path-integration process while suppressing the directional information. Our results suggest that the path integrator cannot process the distance information accumulated by the odometer while ants are deprived of celestial compass information. Hence, during path integration directional cues are a prerequisite for the proper use of travel-distance information by ants.

Introduction

Solitarily foraging *Cataglyphis* ants of the Saharan desert survey their position relative to the nest by “vector navigation” (Wehner 1982, 2003). They continuously update the rotations and translations of their tortuous outbound paths (a process termed “path integration”; Mittelstaedt 1983), and are thereby able to return to the nest on a straight line at any time during their foraging excursions. The compass information needed to accomplish this task is derived from skylight cues including the polarization and spectral gradients in the sky (for a review see Wehner and Srinivasan 2003). The cues involved for the assessment of travel distance, on the other hand, are less clear. Whereas bees estimate the distance flown by measuring the optic flow perceived during flight (Esch and Burns 1995; Srinivasan et al. 1996, 2000; Esch et al. 2001), ants have been shown to be able to gauge the running distance correctly in the

absence of any optic flow-field cues (Ronacher and Wehner 1995; Ronacher et al. 2000). Instead, they seem to acquire the distance information primarily by proprioceptive means (Wohlgenuth et al. 2001, 2002; Thiélin-Bescond and Beugnon 2005). However, how this information is acquired and finally used in path integration remains to be elucidated. In the present account we address the question of whether desert ants, *Cataglyphis fortis*, are able to assess the homing distance correctly if they are partly deprived of directional information during their outbound run.

Materials and methods

The experiments were performed in a salt pan near Maharrès, Tunisia (34°32' N, 10°32' E). In tunnel experiments desert ants, *C. fortis*, were trained to forage within a linear channel, that is, to reach a feeder at a distance of 25 m to the north of the nest entrance (Fig. 1a; for a detailed description of the channel construction see Sommer and Wehner 2004). The channel consisted of alternating open and covered sections of 1.5 m length. Foraging ants were therefore partly deprived of the celestial compass information. A total of eight tunnels resulted in a ratio of 13 m open to 12 m covered sections between the nest and the feeder.

Ants that appeared at the feeder were marked by a day-specific colour code. They were allowed to shuttle back and forth between the nest and the feeder for at least one day, in order to get accustomed to the channel. During this training paradigm the ants will have performed about 20 foraging and subsequent return runs to the feeder and the nest, respectively (Akesson and Wehner 2002). For test runs individual ants were captured at the feeder. After having grasped a biscuit crumb they were released at the northern end of an uncovered test channel arranged in parallel to the training channel (Fig. 1c). There they ran off their global inbound (home) vector, which was the 180° reverse of the immediately preceding outbound (foraging) vector and identical to the inbound vectors of the former home runs. The length of each homing run was measured as the

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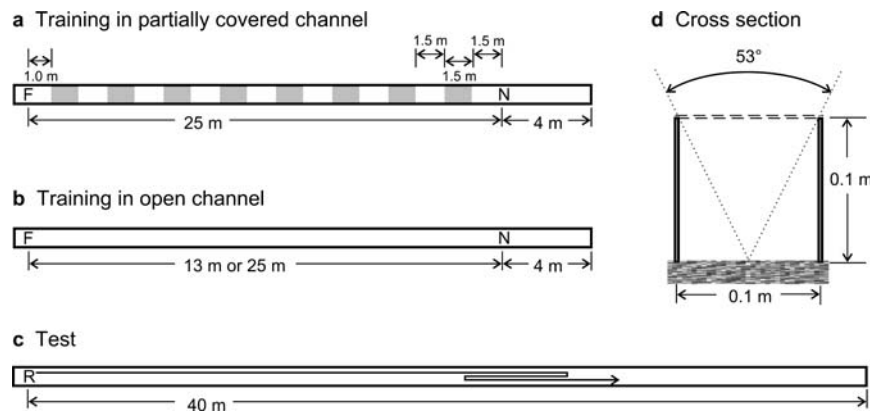


Fig. 1 Schematic representation of the channels used for training and testing foraging desert ants, *C. fortis*; not drawn to scale. **a** Top view of the channel as used in the tunnel-training paradigm. The shaded areas represent the covered sections. The feeder (F) was located to the north of the nest entrance (N). **b** Training channel used for the control experiments. **c** Test channel aligned in parallel to the training channels. The line depicts an ant's homing trajectory start-

ing at the point of release (R) and including the first two U-turns. In all cases north is to the left. **d** Cross-section of training and test channels. The side walls consisted of wooden plates. The same plates were used to cover the tunnel sections (as indicated by the broken lines) in the training paradigm. The ants were running on the desert ground (speckled area)

distance between the point of release and the ant's first U-turn, which indicated the start of the search for the nest entrance (Wehner and Srinivasan 1981). For 3 min the positions of all U-turns were recorded. The ant's uncertainty about the position of the (fictive) nest entrance was measured as the maximum range covered during the 3-min nest search, that is as the distance between the northernmost and the southernmost U-turns.

In two control experiments ants were trained to forage in uncovered channels at either 13 m or 25 m due north (Fig. 1b). The nest-feeder distance in the 13-m control corresponded to the total distance travelled in the uncovered sections of the tunnel experiment. Therefore, the results of the 13-m control and of the tunnel experiment were expected to be similar, if the ants did not include the tunnel sections into their estimate of total distance travelled. Alternatively, if the tunnel sections had been included, the results of the tunnel experiment were expected to be similar to the results of the 25-m control. Distance was measured to the nearest 0.1 m. We tested 25 ants per training condition. Each ant was tested only once.

Multiple comparisons between experiments were performed by using the Tukey–Kramer method for general linear models in SAS 8.2. Because the data differed from normality the values of the first-turn and range variables were rank-transformed before the analyses (SAS Online-Doc, v.8., 1999; SAS Institute, Cary, NC).

Results

As Fig. 2 clearly shows, the ants excluded the distances travelled through the covered channel sections from their estimate of total travel distance. The median lengths of the homing runs were 13.8 m in the tunnel experiment, and 12.9 m and 23.0 m in the 13- and the 25-m control experiments, respectively. Accordingly, in the tunnel experiment

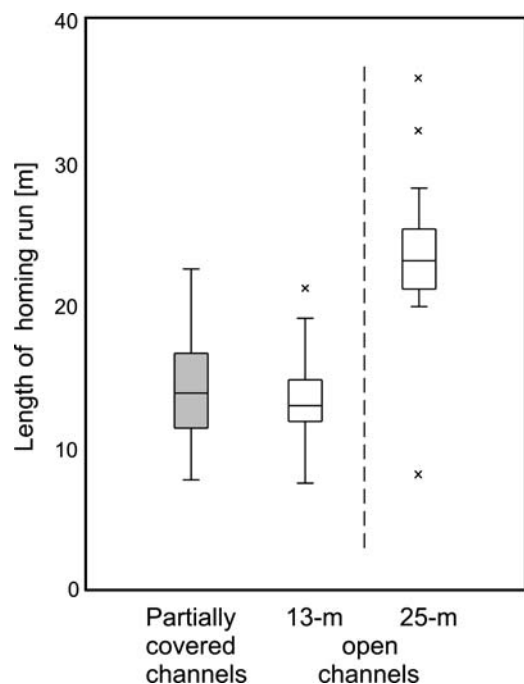


Fig. 2 Lengths of the homing runs performed by ants in the open test channel after training in the repeated-tunnel array or in the 13 and 25-m open channels ($n=25$ each). The dashed line separates statistically homogeneous groups at $\alpha=0.0001$ (Tukey–Kramer method). Zero on the y-axis corresponds to the point of release in the test channel. The lower and upper edges of the boxes depict the first and the third quartiles, respectively. The lines inside the boxes are the medians. Outliers are marked by \times

the ants' uncertainty about the position of the nest entrance was similar to the ants' uncertainty in the 13-m control and hence, lower than in the 25-m control (Fig. 3). The median values of the search ranges were 9.4 m in the tunnel experiment, and 9.3 m and 13.7 m in the 13- and 25-m control experiments, respectively. Taken together, a 25-m outbound run through a channel that was partly (8×1.5 m)

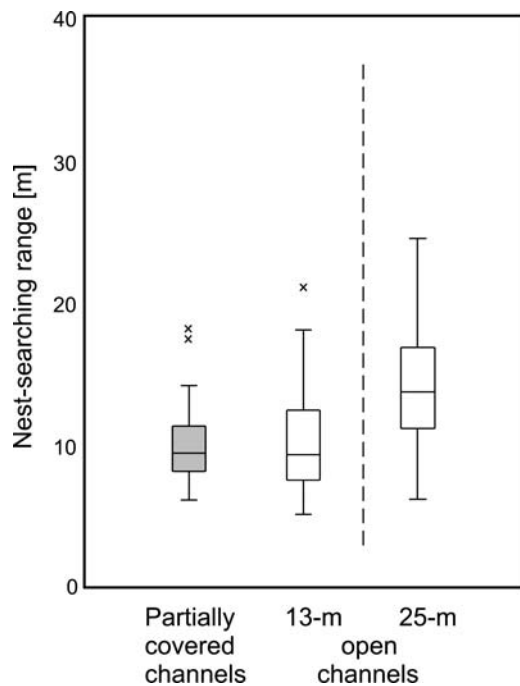


Fig. 3 Nest-searching ranges of ants presented with the same three training paradigms mentioned in Fig. 2 ($n=25$ each). The dashed line separates statistically homogeneous groups at $\alpha=0.005$ (Tukey–Kramer method). For further conventions see Fig. 2

covered induced a homing run of roughly 13 m. This implies that both compass and odometer of the path integrator were inactive or that the output of the still running odometer was stopped every time the compass was inactive while the ants were running through the tunnels.

Discussion

The present account addresses the question of whether desert ants while navigating by path integration are able to assess the length of their home vector correctly if they are partly deprived of compass information. The directional component of the path-integration process was controlled by using linear channel arrangements. This simplified the ants' task and allowed us to focus on the distance component. We demonstrated that ants homing in the test channel undershot the fictive nest entrance (Fig. 2) and that they exhibited a more concentrated search (Fig. 3), if they had been trained in channels that consisted of a sequence of open and covered (tunnel) sections, so that they were partially deprived of skylight vision (i.e. compass information). The magnitude of the undershooting corresponded approximately to the total length of the tunnel sections that the ants had to pass when they ran back and forth between the nest and the feeder during training. This result implies that either the ants' odometer could not have recorded the distances covered by the ants in the tunnels, because the essential cues might not have been available, or the ants' path integrator had not been able to process the distance information acquired by the odometer, because

there was no simultaneous input from the compass, that is no directional information accompanying the distance information. For the following reason we favour the latter explanation.

While the ants were running through the tunnels, they had only reduced access, or no access at all, to two sources of information which are known to play a role in the path-integration process: celestial compass information and, to a lesser extent, self-induced optic flow. As has been shown earlier, in *C. fortis* ventral optic image flow can assist in gauging distances travelled (Ronacher and Wehner 1995). However, even if such cues are absent, the ants are still able to home correctly. This implies that, in assessing travel distance, ants can exploit other sources of information. Idiothetic (proprioceptive) cues and efference copies of motor commands are the most likely candidates of such sources of information (Ronacher et al. 2000; Wohlgenuth et al. 2001, 2002; Thiélin-Bescond and Beugnon 2005). Since such cues were fully available to the ants when they were running through the tunnels, the shortened homing runs recorded in the tunnel experiments must be explained by other means, e.g. by the lack of celestial compass information.

Tests with different ant species in darkness revealed different results. Grass ants, *Tetramorium caespitum*, were unable to home correctly in the dark after an outbound run in daylight (Shen et al. 1998). On the other hand, *Cataglyphis cursor* foragers managed to home correctly in darkness after they had repeatedly been trained to cover a short (0.6-m) homing distance in the light (Thiélin-Bescond and Beugnon 2005). Third, as shown in the present account, *C. fortis* foragers did not integrate those distance components into their estimate of total distance travelled that had been covered in the absence of skylight compass cues.

The somewhat surprising success of the *C. cursor* foragers mentioned above might be due to the fact that those ants were trained (in daylight) in the test channel until they chose the correct exit, that is the one that led them to the nest, six times in a row (Thiélin-Bescond and Beugnon 2005). The fact that they were still able to home correctly in darkness suggests that they used idiothetic information. However, 46 out of 47 ants chose the wrong exit during the first test trial in daylight. Had they simply used their path integrator, they should have been able to choose the correct distance on their first return run. That they did not implies that they obviously had learnt to apply a particular strategy to cover the correct distance. What strategy they had acquired during the repeated training trials (about 30 trials per ant) remains elusive. On the other hand, the failure of *T. caespitum* (to home in darkness) and of *C. fortis* (to take into account those distances from the vector-navigation process that have been covered in the dark) indicates that visual input is a prerequisite for the path integrator to operate, as it has previously been suggested for bumblebees (Chittka et al. 1999). Hence, our results are in accord with results obtained with a different experimental paradigm in honey bees, *Apis mellifera* (Collett et al. 1996). They support the view that the processing of distance information by the path integrator is depending on simultaneously obtained directional information. We assume that the insect's path

integrator is updated only if it receives information from both the compass and the odometer.

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